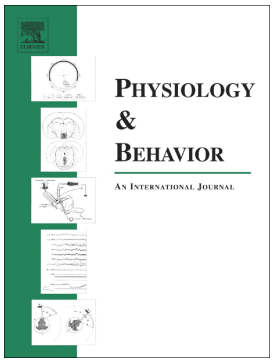

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Environmental and physiological determinants of huddling behavior of molting female southern elephant seals (*Mirounga leonina*)

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Abstract

While endotherms can rely on their insulation to reduce heat loss to adapt to cold environments, renewing of fur during molt impairs insulation while they have to perfuse the periphery to support epidermal tissues. The southern elephant seal *Mirounga leonina* undertakes an annual catastrophic molt while fasting on land in a wet, windy and cold environment. However, southern elephant seals show characteristic aggregation patterns that are predicted to reduce high metabolic costs during the molt. Between 2012 and 2016, 59 female elephant seals were tracked on land during their molt to study their aggregation behavior in relation to molt stage, habitat type and local weather conditions. Infrared thermography and stomach temperature loggers were used to observe variation in body surface and internal temperature in relation to molt stage and aggregation behavior. We found that thermal constraints varied during the molt, with a peak in surface temperature during the mid-stage of the molt. Wallows (mud pools) appear as favorable habitat to aggregate while molting. Indeed, wallows offered a warmer microclimate with greater ground temperature and lower wind speed. Moreover, there was a greater proportion of aggregated seals and larger group size in wallows. These aggregation patterns in wallows were influenced by local weather such that a greater proportion of seals were located in the center of the aggregation, and larger group size occurred during days of unfavorable meteorological conditions. We also observed a higher proportion of seals at mid-stage of molt amongst aggregated seals compared to isolated individuals. This aggregation behavior may reduce the cost of thermogenesis as surface body temperature and stomach temperature were cooler by 1.0°C and 1.5°C, respectively, in aggregated compared to isolated seals. As a consequence, huddling behavior may be thermally advantageous for female southern elephant seals during the molt.

Abbreviations

- T_a air temperature
- T_g ground (substrate) temperature
- T_b body surface temperature
- T_f surface temperature at the insertion point of the lateral flipper
- T_h surface temperature of the aggregation (huddle)
- T_{stom} stomach temperature
- $\Delta T_b = T_b - T_a$ gradient of body surface temperature
- $\Delta T_f = T_f - T_a$ gradient of flipper surface temperature (at the insertion point of the lateral flipper)
- $\Delta T_h = T_h - T_a$ gradient of surface temperature of the aggregation (huddle)

1. Introduction

In order to maintain a high and relatively constant body temperature, endotherms living in a cold environment must increase their insulation to compensate for heat loss. This adaptive insulation allows them to have an extended thermoneutral zone, without increasing their metabolic rate (Scholander et al., 1950; Schmidt-Nielsen, 1997; Willmer et al., 2005; Clarke, 2017). Most Antarctic and Sub-Antarctic birds and mammals forage at sea and breed or molt while fasting on land, thereby experiencing contrasting periods of energy use and environmental conditions. Living in different physical and thermal environments requires morphological, physiological and behavioral adaptations. For example, pinnipeds are adapted to heat conservation in a cold environment because of low surface area to volume ratio, thick layer of subcutaneous blubber, and vascular peripheral anastomoses regulating cutaneous blood perfusion (Schmidt-Nielsen, 1997; Mauck et al., 2003). However, behavioral adaptations to minimize heat loss are also widespread in the wild. Indeed, social thermoregulation (huddling), widely used by endotherms, allows metabolic savings by reducing thermoregulatory costs (Gilbert et al., 2010). Reducing heat loss by huddling permits reallocation of energy savings to other physiological processes (*e.g.* reproduction or growth). However, during the molt, heat loss increases as blood flow to peripheral tissues must be maintained to support tissue growth and regeneration.

Southern elephant seals *Mirounga leonina* experience an annual 'catastrophic' molt lasting one month, not only renewing their hair but also their cornified epidermis (Ling, 1968). During this period, molting elephant seals are likely to be more sensitive to heat loss because of their inability to avoid peripheral vascular circulation. The molt is particularly costly in this species: molt metabolic rate in southern elephant seals is estimated to be 2-3 times greater than resting metabolic rate, and appears to be more energetically costly than in northern elephant seals (*Mirounga angustirostris*; Worthy et al., 1992; Boyd et al., 1993).

However, decreases in metabolism during the molt have been described in other related species when captive during the same period (harbour seals *Phoca vitulina*: Ashwell-Erickson et al., 1986; Rosen and Renouf, 1998). While molting, female body mass loss averages 4-5 kg per day in southern elephant seals, mainly fat from blubber metabolism (Boyd et al., 1993; Hindell et al., 1994; Carlini et al., 1999; Postma et al., 2013). Paterson et al. (2012) showed that heat loss of phocids increases during the molt, with an increase in skin temperature due to perfusion by vasodilation through the blubber layer to supply nutrients for epidermis renewal (Ashwell-Erickson et al., 1986). Feltz and Fay (1966) demonstrated *in vitro* that the epidermal cells of phocids require a minimum temperature of 17°C, and an optimal temperature of 37°C, to grow. The high metabolic rate observed in southern elephant seals while molting could be related to the fact that they molt in a cold environment with increased thermoregulatory costs.

Southern elephant seals aggregate in large groups, mostly in mud pools (wallows), while molting on land (Laws, 1956; Boyd et al., 1993; Chaise et al., 2018) and this behavior seems to be influenced by local weather conditions (Cruwys and Davis 1995; Chaise et al., 2018). In California sea lions *Zalophus californianus*, huddling behavior increases in colder weather and allows animals aggregated in the middle of a group to maintain a higher surface temperature than the substrate compared to isolated individuals (Liwanag et al., 2014). In the same way, huddling individuals of most mammal and bird species maintain a higher and more constant core and surface body temperatures than isolated individuals (Gilbert et al., 2010). However, a higher gradient between body surface temperature and ambient temperature would result in increased heat loss and associated thermoregulatory cost (Canals et al., 1989; McCafferty et al., 2011). In contrast, Gilbert et al. (2007) showed that microclimate created by huddling (up to 37.5°C within tight huddles) allows male emperor penguins *Aptenodytes forsteri* to save energy during their breeding fast through decreases in core temperature. We therefore predict that aggregated adult southern elephant seals benefit from huddling, either

by the maintenance of a higher body temperature allowing a more rapid molt, or a lowering of thermal gradients between surface and ambient temperature, allowing energy savings during the molt.

The aim of this study was therefore to evaluate thermal consequences of aggregation in molting females, using infrared thermography as a non-invasive technique to measure body surface temperature, concurrently with the recording of internal temperature, of free-ranging pinnipeds (Mauck et al., 2003; McCafferty et al., 2005; Norris et al., 2010; Paterson et al., 2012; Liwanag et al., 2014; Codde et al., 2016). We expect aggregation behavior to be more intense in wallows, where elephant seals have been observed aggregating (Laws, 1956; Boyd et al., 1993; Chaise et al., 2018), compared to other habitats (grass and rocky beach), as wallows could be a warmer habitat for molting. We also expect that aggregation behavior increases in the middle of the molt (corresponding to a peak in surface temperature; Paterson et al., 2012) and when weather conditions are deteriorating (Liwanag et al., 2014). We therefore predict that aggregation allows elephant seals to modulate their internal and surface temperatures to reduce the cost of thermoregulation and increase their rate of molt in order to minimize mass loss during the molting fast.

2. Material and methods

2.1. Data collection

2.1.1. Study site

Field work took place during four molting seasons of adult female elephant seals in 2012 and 2014-16 (Table 1), at the colony of Pointe Suzanne (49°26'S, 70°26'E) in Kerguelen Island (French Southern and Antarctic Lands). Based on the assumption that different areas would offer different thermal environments, the study site was divided into three different habitats based on substrate type and topography: stony beach, grassland and wallows (mud pools without vegetation created by aggregation of molting elephant seals within grassland).

Years	**Number of transects scans (grass/beach)**	**Number of quadrat scans (wallows)**	**Number of tracked/recaptured [equipped] females**	**Number of observations**	**Tracking duration (days)**
18 Jan to 19 Feb 2012	30/30	14	15/12 [0]	5.7 ± 3.3	13.7 ± 3.8
29 Dec 2013 to 1 Mar 2014	39/40	33	25/21 [3]	5.2 ± 2.9	8.6 ± 3.3
23 Dec 2014 to 15 Jan	11/11	12	7/7 [2]	1.3 ± 0.5	4.1 ± 1.0

2015					
22 Jan to 27 Feb 2016	/	/	12/13 [4]	4.5 ± 1.6	6.1 ± 1.9

Table 1 Dates of transects and quadrat scans, number of female elephant seals recaptured, tracked and equipped with stomach temperature pills, mean number of observations and tracking duration (days).

2.1.2. Population surveys

These data are based on daily observations of unidentified female elephant seals in defined areas. Two strip transects on beach habitat (49°26'02''S, 70°26'23''E - 49°25'59''S, 70°26'17''E; 150 m long; ± 10 m from the line transect) and grass habitat (49°26'00''S, 70°26'16''E - 49°26'03''S, 70°26'22''E; 150 m long; ± 10 m from the line transect) and one quadrat in wallow habitat (49°26'16''S, 70°25'59''E - 49°26'20''S, 70°25'45''E - 49°26'32''S, 70°25'46''E - 49°26'26''S, 70°26'09''E; 0.14 km²) were defined to study the influence of habitat type and local meteorological parameters on elephant seal aggregation behavior during the molt. The transects and quadrat were scanned daily for a total of 220 scans between 2012 and 2014-15 (Table 1). At the start of each scan, meteorological variables, including air temperature (T_a, °C), ground temperature (T_g, °C; 5 cm depth; from 2014), relative humidity (%), wind speed ($m.s^{-1}$) and solar radiation ($W.m^{-2}$), were measured using hand-held devices (Kestrel 3000 Pocket Weather Meter; pyranometer SKS111, Skye Instruments Ltd, Llandrindod Wells, UK). During each scan, we recorded the molt stage of each seal observed (mainly adult females, with possible presence of few juveniles and males). We defined three molt stages, assessed by the percentage of old hair/skin shed (0 %: no old hair shed to 100 %: all old hair shed; ± 10 %; Fig.1): this was then divided into initial stage (0-40 % of old hair shed; still largely covered with old hair), mid-stage (50-80 %; most of old hair shed and new hair still not grown) and final stage (90-100 %; new hair growing). We recorded whether the observed seal was aggregated or isolated, where an aggregation was defined when at least two elephant seals were in physical contact. In an aggregation, an elephant seal was considered in a peripheral position (P) when only one of its sides was in physical contact with others, otherwise it was recorded as in a central position (C). We also calculated an aggregation score (number of aggregated seals/total number of seals) for each transect and quadrat, the size of each aggregation (number of aggregated seals) and the C/P

ratio of the aggregation (number of central seals/number of peripheral seals). Thermal (± 0.1°C) and visual images were taken (ThermaCAM® P25, FLIR Systems, accuracy ±2°C; Lumix DMC-FS35 EF-K, Panasonic; TG-4, Olympus) for each aggregation or isolated female.

Figure 1 Molting female southern elephant seals shedding old skin and hair: initial stage (A), mid-stage (B) and final stage of molt (C).

2.1.3. Individual data

Between 2012 and 2016, 59 adult females were captured at the initial stage of molt, then tracked during 4.7 ± 2.9 days (range 1-13 daily observations), and 53 were recaptured at the final stage of molt (Table 1), 8.6 ± 4.3 days after their first capture (range 3-20 days). Elephant seals were captured on the colony, anaesthetized using tiletamine and zolazepam (McMahon et al., 2000; Chaise et al., 2017) and tagged on one hind flipper with plastic identification tag (Dalton Tags, UK). Females were weighed at capture and recapture (HST Mini-Weigher, 0-1000 kg ± 0.5 kg, HST Scales UK Ltd) to calculate body mass loss ($kg.d^{-1}$). All captured seals were equipped with VHF transmitters (Series MM300 Marine Mammal Headmount, model MM340B, 7.1 x 3.5 x 2.1 cm; 92 g, Advanced Telemetry Systems, USA) to track them on land, and nine individuals were equipped with stomach temperature pills and

time-depth recorders (TDR-STP-207D; MK10-L/SPLASH10-309, 76 x 56 x 32 mm, 125 g, Wildlife Computers, USA) between 2014 and 2016. Stomach temperature pills were placed in the stomach under anesthesia using a lubricated flexible tube, and recorder tags were fixed on the head with epoxy bi-composed glue Araldite®. Stomach pills were set up to record stomach temperature (T_{stom}) every 10 s. Temperature was recorded during 4.9 ± 2.7 days (range 1-10 days) before the signal was lost, due to natural passage of pill through the gut. For each observation of a tracked elephant seal, digital and thermal images were taken, and molt stage and aggregation status (aggregated or isolated) were determined. In order to compare stomach temperatures between aggregated and isolated individuals, we selected stomach temperature data at the time when individuals were observed and photographed (six individuals out of nine equipped). As we recorded paired data (in both positions: aggregated vs. isolated) for very few individuals (half of our stomach temperature data were unpaired) we assumed independence for statistical analyses. We calculated the individual aggregation rate (number of observations in aggregation/total number of observations). We also recorded meteorological variables (air and ground temperature, relative humidity, wind speed and solar radiation) close to the seal.

2.2. Data analyses

2.2.1. Thermal images

Thermal images were analyzed using the software ThermaCAM® Researcher Pro 2.10 (FLIR Systems, USA). For each image, we specified air temperature (*i.e.* measured air temperature T_a, ^oC), relative humidity (%), distance (m) and mammal pelage emissivity of 0.98 (Humes et al., 1994; Norris et al. 2010; McCafferty et al., 2011). For measurements on caught individuals, mean body surface temperature T_b (^oC) was determined by fitting a

polygon around the visible body of the seal, and by measuring mean fore flipper surface temperature T_f (^oC) from spot measurement at the axillary, as this is an important thermal window (Mauck et al., 2003; Nienaber et al., 2010) (Fig.2A). For transects and quadrat data, mean surface temperature of the aggregation T_h (^oC) was determined by fitting a polygon around all visible bodies of aggregated seals and T_f from spot measurement from visible axillary of each seal (Fig.2B). Obvious wet seals and images out of focus were discarded from analysis. We used thermal gradients ($\Delta T_{b,f,h} = T_{b,f,h} - T_a(°C)$) for thermal analysis of surface temperatures.

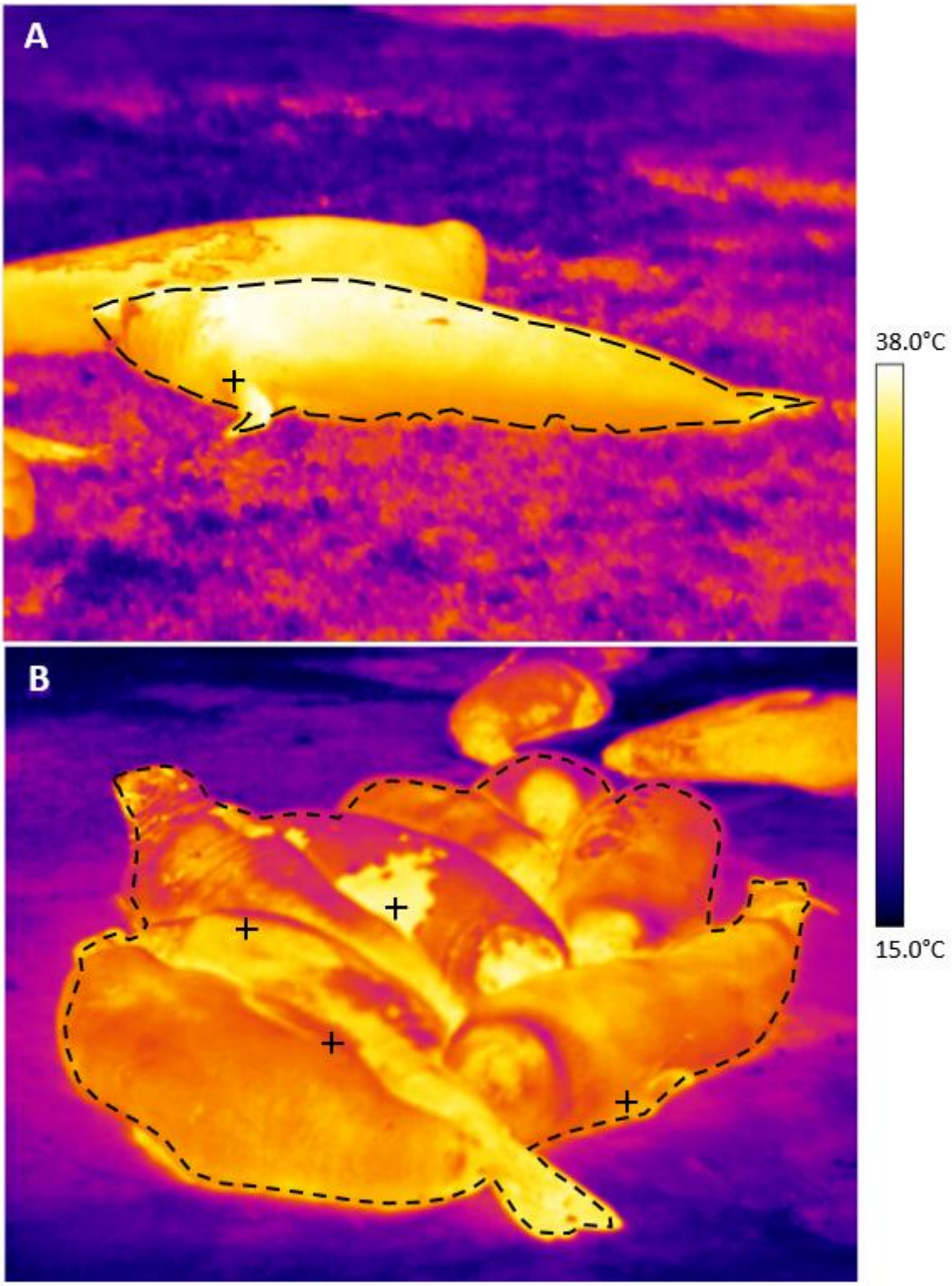

Figure 2 Analyses of thermal images from observations of tracked individuals (A) and daily transects or quadrat scans (B). In A, body surface temperature (T_b) is the average temperature

of the dotted polygon (outline of the body) and fore flipper surface temperature (T_f) is the pixel temperature of the cross point. In B, surface temperature of the huddle (T_h) is the average temperature of the dotted polygon (outline of the aggregation) and fore flipper surface temperatures of visible aggregated seals (T_f) are pixel temperatures of the respective cross points (ThermaCAM® Researcher Pro 2.10; FLIR Systems, USA).

2.2.2. Surface body temperature of population surveys data

Correlation between T_b and T_f of individuals in 2012 and 2014 was analyzed using a linear model (R^2 = 0.74, F = 247.2, df = 87, $P < 0.0001$) after normality and equality of variances were verified. We therefore used the linear regression for individuals (T_b = 4.59 + 0.81 * T_f (°C)) to estimate body surface temperature (T_b) from lateral flipper surface temperature (T_f) recorded in seals observed during transects and quadrat scans.

2.2.3. Weather index

A temporary automatic weather station (MiniMet, Skye Instruments Ltd) located at Pointe Suzanne (49°26’18’’S, 70°26’31’’E) recorded air temperature (°C), relative humidity (%), wind speed ($m.s^{-1}$), solar radiation ($W.m^{-2}$) and precipitation (mm) every 30 min during field seasons and summarized to give daily averages and daily rainfall. We used a centered-scale Principal Component Analysis (PCA) to determine an integrated weather index (from air temperature, relative humidity, wind speed, solar radiation, and precipitation) in order to examine effects of weather on aggregation behavior (dudi.pca in ade4 package; Supplementary material S1). The first component (PC1) accounted for 39 % of the variation, the second (PC2) for 23 % and the third (PC3) for 19 %. PC1 received major positive loadings from relative humidity and precipitation and a major negative loading from solar

radiation. PC2 received a major positive loading from air temperature. PC3 received a major positive loading from wind speed (Supplementary material S1). Principal components were then transformed to binary factors, based on their respective median values, to distinguish days of 'bad weather' (for days with PC1 value > PC1 median value, PC2 value < PC2 median and PC3 value > PC3 median; high relative humidity, low solar radiation, low air temperature and high wind speed) from days of 'good weather' (for days with PC1 value < PC1 median value, PC2 value > PC2 median and PC3 value < PC3 median; low relative humidity, high solar radiation, high air temperature and low wind speed). For 11 % of data (11 days), variations of PC2 or PC3 differed from PC1 (*e.g.* days with PC1 value < PC1 median value, PC2 value < PC2 median and PC3 value < PC3 median; or days with PC1 value < PC1 median value, PC2 value > PC2 median and PC3 value > PC3 median; or days with PC1 value > PC1 median value, PC2 value < PC2 median and PC3 value < PC3 median). In those cases, classification of weather index was based on PC1 value (accounting for 39 % of the global weather variation).

2.2.4. Statistical analysis

Generalized linear mixed models (GLMMs) were used to analyze aggregation behavior of elephant seals in transects and quadrat (aggregation rate, aggregation size and C/P ratio) in relation to habitat type (grass, beach, wallow) and weather index ("good weather" and "bad weather" days) as fixed effects (with size of aggregations as covariate for C/P ratio of aggregations), and with date as random effect. A similar model was used afterwards to analyze, for each habitat separately, the effect of meteorological parameters (air temperature, relative humidity, solar radiation and wind speed) on aggregation behavior. GLMMs were also used to analyze the effect of aggregation behavior (aggregated vs. isolated, and central vs. peripheral individuals) on the gradient of flipper surface temperature (ΔT_f), the effect of

aggregation size on surface temperature of aggregated individuals (ΔT_h), and the effect of stages of molt on body surface temperature (ΔT_b). Analyses of aggregation effect on surface temperatures included meteorological variables (relative humidity, solar radiation and wind speed) as covariates, and date as a random effect. Aggregation identity number was added as a random effect for ΔT_f analyses, and aggregation size was added as a covariate for comparison of ΔT_f between central and peripheral individuals. Models were fitted with a Poisson distribution and final GLMMs were selected based on Akaike Information Criterion (AIC) for removal of non-significant effects and interactions. We used Wilcoxon tests to compare stomach temperature (T_{stom}) between aggregated or isolated, and central or peripheral elephant seals. Local meteorological variables between habitats were compared using Kruskal-Wallis rank sum tests followed by a multiple comparison test when significant (adjusted pairwise comparisons; kruskalmc in pgirmess package). We used a Kolmogorov-Smirnov test to compare distribution of molt stages between aggregated and isolated elephant seals during transects and quadrat scans. Spearman's rank coefficient tests were used to analyze correlations between body condition variations (initial body mass and daily body mass loss), molt rate, and aggregation behavior (individual relative aggregation rate). Results were expressed as mean ± standard deviation (SD). All statistical analyses were performed with R statistical software (R Development Core Team, version 3.5.1; RStudio Inc., version 1.1.456) and statistical significance was accepted at $P < 0.05$.

3. Results

3.1. Thermal environment of molting elephant seals: habitats and stage of molt

When we compared meteorological variables between transects and quadrat in 2012 and 2014-15, we observed that the difference between ground temperature and air temperature (T_g - T_a) was greater in wallows compared to beach and grass habitats, while no difference

was found between grass and beach habitats (N = 73, χ^2 = 24.92, df = 2, $P < 0.0001$; Table 2). Differences in ground temperature were found between all three habitats, wallows being the warmest (N = 73, χ^2 = 35.19, df = 2, $P < 0.0001$) while air temperature was not different between the three habitats (N = 147, χ^2 = 0.33, df = 2, P = 0.85; Table 2). Wind speed was lower in wallows compared to grass habitat (N = 145, χ^2 = 6.24, df = 2, P = 0.04; Table 2) but not when compared to beach habitat. Relative humidity and solar radiation were similar between all three habitats (N = 144, χ^2 = 0.03, df = 2, P = 0.99; N = 139, χ^2 = 2.4, df = 2, P = 0.31).

Habitat	**Scans (days)**	**Air Temp. T_a (°C)**	**Ground Temp. T_g (°C)**	**T_s - T_a (°C)**	**Relative Humidity (%)**	**Wind speed ($m.s^{-1}$)**	**Solar radiation ($W.m^{-2}$)**
Grass	54	9.0 ± 3.0	7.6 ± 1.5 [a]	-0.9 ± 2.3 [a]	71 ± 14	4.8 ± 2.9 [a]	569 ± 363
Beach	54	9.4 ± 3.1	9.9 ± 2.7 [b]	0.5 ± 2.8 [a]	73 ± 26	4.6 ± 3.1 [a, b]	555 ± 387
Wallows	39	9.2 ± 2.9	14.1 ± 5.1 [c]	5.4 ± 5.6 [b]	70 ± 13	3.4 ± 2.3 [b]	464 ± 366

Table 2 Local meteorological variables (mean ± SD) recorded at the start of daily transects and quadrat scans (2012 and 2014-15) for each habitat type and significant differences (post-hoc test: $P < 0.05$). We recorded a mean of 5 ± 2 rainy days per year during scans over the field session.

We compared body surface temperature between the three stages of molt for individual (2012 and 2014, N = 134) and population surveys data (2012 and 2014-15, N =

708). The thermal gradient of body surface temperature was greatest by 2.0 ± 3.6°C during mid-stage compared to initial (estimate ± SD = 0.12 ± 0.06, z = 2.18, *P* = 0.03) and final stages (estimate ± SD = 0.12 ± 0.05, z = 2.55, *P* = 0.01) but no significant difference was found between initial and final stage of molt (estimate ± SD = 0.006 ± 0.04, z = 0.17, *P* = 0.87; Fig.3).

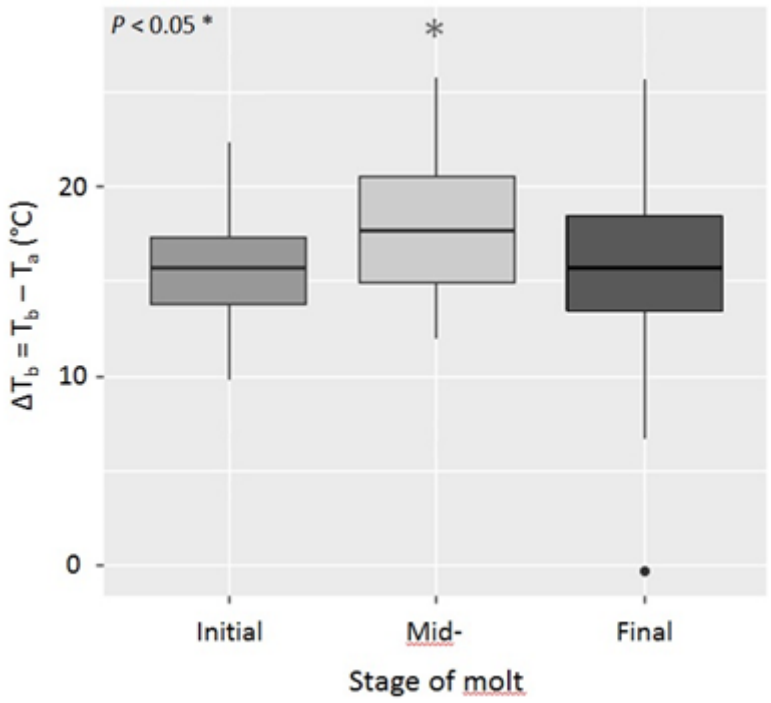

Figure 3 Body surface temperature (ΔT_b) gradient between body surface temperature (T_b) and air temperature (T_a) during the molt from individual data (2012 and 2014) and population surveys data (from strip transects and quadrat counts; 2012 and 2014-15; bold lines: medians; box lengths: interquartile ranges between first and third quartiles IQR = (Q3-Q1); whiskers: Q1-1.5*IQR and Q3+1.5*IQR). Mean T_a = 9.7°C (N = 842).

3.2.Influence of molt, habitat and weather on aggregation behavior

Distribution of molt stages varied between aggregated and isolated seals observed on transects and the quadrat (D = 0.18, *P* < 0.0001). We observed a higher proportion of seals at

mid-stage of molt amongst aggregated seals compared to isolated seals, and mainly seals at initial or final stage of molt amongst isolated seals (Fig.4).

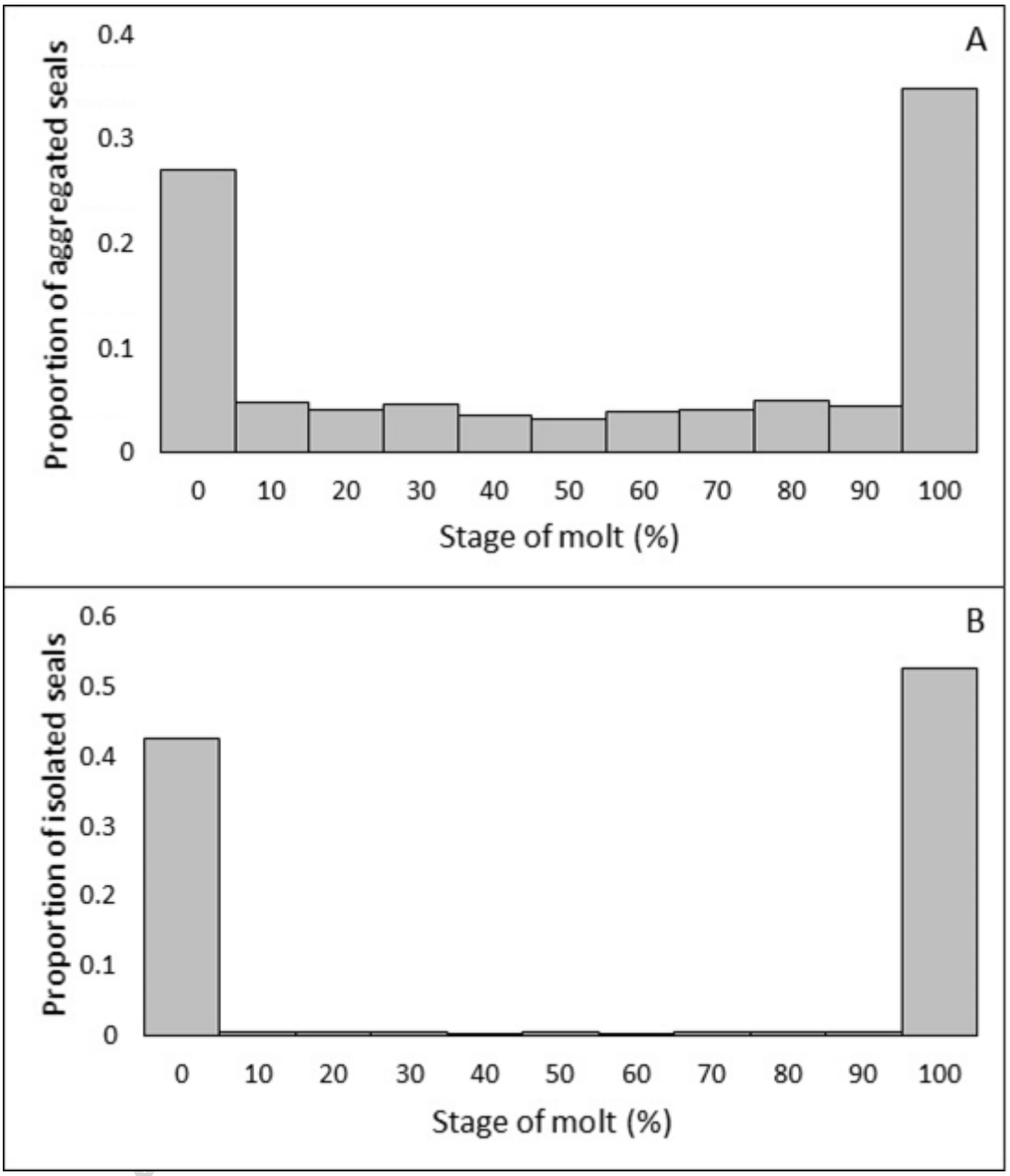

Figure 4 Distribution of molt stages amongst aggregated seals (A) and isolated seals (B) expressed as a proportion of the total number of observed seals during transects and quadrat scans between 2012 and 2015.

Huddling behavior of molting female elephant seals (population based-data) was influenced by habitat type and local weather conditions. The proportion of aggregated seals (*i.e.* aggregation rate, N = 176; Fig.5A) was less in grass (mean ± SD = 0.5 ± 0.2; estimate ± SD = -0.58 ± 0.08, z = -7.41, $P < 0.0001$) and beach habitats (0.6 ± 0.2; estimate ± SD = -0.41 ± 0.07, z = -5.74, $P < 0.0001$) compared to wallows (0.9 ± 0.2), and less in grass compared to beach habitats (estimate ± SD = -0.16 ± 0.06, z = - 2.63, $P = 0.009$; Fig.5A). The model also estimated that aggregation rate was marginally higher during days of "bad weather" compared to days of "good weather", for all habitats (estimate ± SD = 0.12 ± 0.07, z = -1.88, $P = 0.06$) but this result was non-significant. When we compared aggregation rate with weather index for each habitat, we observed that seals aggregated more in grass habitat during "bad weather" days (estimate ± SD = 0.24 ± 0,11, z = 2.15, $P = 0.03$; Fig.5A). Indeed, when we analyzed the effect of meteorological parameters, we observed that seals aggregate more in grass habitat with increased wind speed (estimate ± SD = 0.05 ± 0.02, z = 2.30, $P = 0.02$) and less with increased solar radiation (estimate ± SD = -0.0004 ± 0.0002, z = -2.49, $P = 0.01$). In the same way, our results showed that elephant seals aggregate less in beach habitat with increased solar radiation (estimate ± SD = - 0.0003 ± 0.0001, z = -1.97, $P = 0.049$) and more in wallows with increased relative humidity (estimate ± SD = 0.005 ± 0.002, z = 2.18, $P = 0.03$).

The number of elephant seals per aggregation (*i.e.* aggregation size, N = 754) was less in grass (mean ± SD = 3.1 ± 1.5; estimate ± SD = -1.03 ± 0.15, z = -6.66, $P < 0.0001$) and beach habitats (4.8 ± 6.9; estimate ± SD = -0.78 ± 0.15, z = -5.36, $P < 0.0001$) compared to wallows (9.4 ± 8.7), and less in grass compared to beach habitats (estimate ± SD = -0.25 ± 0.10, z = -2.44, $P = 0.02$; Fig.5B). The model also estimated that aggregation size was greater during "bad weather" days compared to "good weather" days, regardless of habitat types (estimate ± SD = 0.32 ± 0.16, z = 2.05, $P = 0.04$). Moreover, the model estimated that the difference in aggregation size between wallows and grass habitat was increased during days

of "bad weather". Indeed, when we analyzed the effect of the weather for each habitat, aggregation size increased in wallows with increased relative humidity (estimate ± SD = 0.01 ± 0.006, z = 2.33, $P < 0.05$; Fig.5B) and the same tendency was observed in beach habitat (estimate ± SD = 0.01 ± 0.006, z = 1.95, $P = 0.05$). In comparison, aggregation size in grass habitat marginally increased with increased wind speed (estimate ± SD = 0.02 ± 0.01, z = 1.85, $P = 0.06$), but this result was non-significant.

To study the influence of habitat and weather on C/P ratio, we considered aggregation size as a covariate in the model, since the C/P ratio increased with aggregation size (estimate ± SD = 0.07 ± 0.005, z = 13.90, $P < 0.0001$; N = 689). The model estimated that there were less seals in a central position compared to peripheral positions in wallows compared to grass habitat (estimate ± SD = -1.82 ± 0.23, z = -8.03, $P < 0.0001$) and beach habitat (estimate ± SD = -0.42 ± 0.17, z = -2.45, $P = 0.01$) but no difference between grass and beach habitats (estimate ± SD = 0.09 ± 0.13, z = 0.71, $P = 0.48$). Moreover, the difference in C/P ratio between wallows and grass habitat increased with increased aggregation size (estimate ± SD = 0.29 ± 0.03, z = 8.27, $P < 0.0001$). There was no general effect of weather index on aggregation C/P ratio (estimate ± SD = 0.03 ± 0.13, z = 0.20, $P = 0.84$). However, when analyzed per habitat, aggregation C/P ratio increased in grass habitat with increased relative humidity (estimate ± SD = 0.02 ± 0.006, z = 2.38, $P = 0.02$), and this effect was more important when aggregation size increased (estimate ± SD = 0.006 ± 0.002, z = 2.34, $P = 0.02$). In comparison, C/P ratio marginally increased in wallows, but non-significantly, with increased wind speed (estimate ± SD = 0.05 ± 0.03, z = 1.77, $P = 0.08$), and there was no effect of weather in beach habitat.

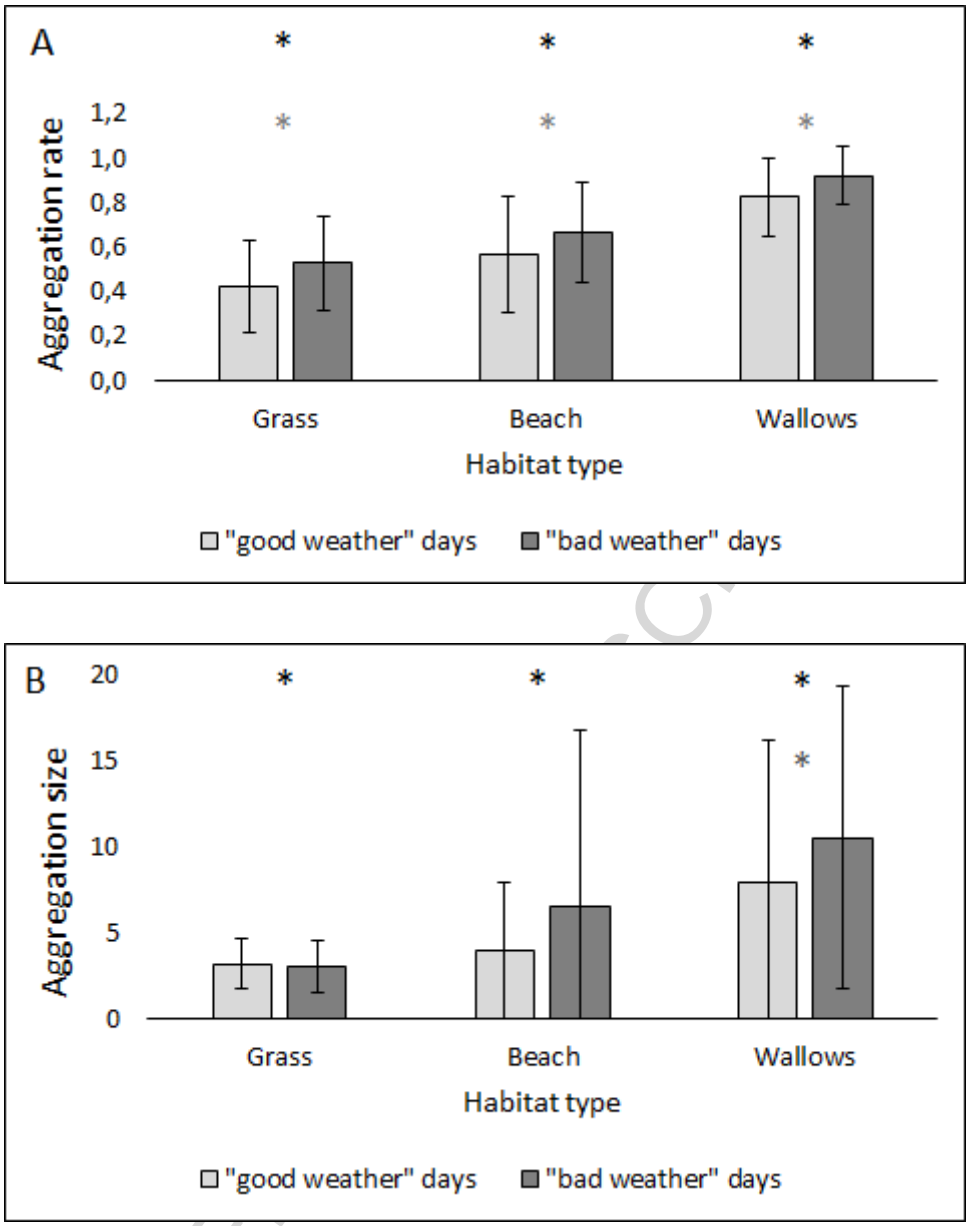

Figure 5 Variation in aggregation rate (number of aggregated seals / total number of seals; A) and aggregation size (number of aggregated seals; B) between habitats (statistical significance $P < 0.05$: black asterisk) and influence of weather conditions (*i.e.* weather index or meteorological variables) per habitat (statistical significance $P < 0.05$: grey asterisk) (population surveys data from 2012 and 2014-15).

3.3.Aggregation behavior and body temperature

In wallows, gradient of body surface temperature of aggregated individuals ($\Delta T_h = T_h$ - Ta; 15.2 ± 3.4°C) decreased with aggregation size (estimate ± SD = -0.006 ± 0.003, z = -2.01, $P = 0.045$). In comparison, no significant relationship was found between gradient and aggregation size in grass (estimate ± SD = -0.003 ± 0.02, z = -0.19, $P = 0.85$) and beach (estimate ± SD = -0.002 ± 0.007, z = -0.31, $P = 0.75$) habitats.

In grass habitat, gradient of surface flipper temperature of aggregated elephant seals (15.8 ± 4.3°C) observed during transects scans was lower than gradient of isolated seals (17.2 ± 4.5°C; estimate ± SD = -0.08 ± 0.03, z = -2.40, $P = 0.02$; N = 376). But no difference of temperature was revealed between aggregated and isolated animals in beach habitat (aggregated: 15.5 ± 4.3°C; isolated: 16.2 ± 3.8°C; estimate ± SD = -0.003 ± 0.03, z = -0.10, $P = 0.92$; N = 419) or wallows (aggregated: 17.6 ± 4.1°C; isolated: 17.7 ± 3.7°C; estimate ± SD = 0.01 ± 0.05, z = 0.24, $P = 0.81$; N = 189).

No significant difference was found in gradient of flipper surface temperature between central and peripheral seals observed in aggregations (grass: central: 15.6 ± 3.6°C, peripheral: 15.7 ± 4.4°C, estimate ± SD = 0.03 ± 0.08, z = 0.36, $P = 0.72$, N = 103; beach: central: 16.6 ± 3.4°C, peripheral: 15.3 ± 4.5°C, estimate ± SD = -0.06 ± 0.07, z = -0.90, $P = 0.37$, N = 134; wallows: central: 17.6 ± 4.3°C, peripheral: 17.7 ± 4.1°C, estimate ± SD = 0.002 ± 0.04, z = 0.05, $P = 0.96$, N = 156).

Stomach temperatures averaged 36.6 ± 0.5°C (range 30.3-39.9°C). We did not observe major or constant variations in average or extreme values over time before the signal was lost. Stomach temperatures recorded for individuals observed in aggregation were lower than

stomach temperatures recorded for isolated individuals (N = 12, W = 3, $P = 0.02$). Both aggregated and isolated individuals were observed in wallows or grass habitat.

3.4. Aggregation, body mass and molt

Females at first capture weighed 316.2 ± 34.4 kg (range 259-410 kg) and their body mass loss during the molt averaged 3.3 ± 0.9 $kg.d^{-1}$ (range 1.7-6.7 $kg.d^{-1}$). Mean relative individual aggregation rate (number of observations in aggregation / total number of observations) was 0.69 ± 0.21 and molt rate averaged 10.0 ± 3.7 $\%.d^{-1}$ (range 2.0-17.5 $\%.d^{-1}$).

We found no significant correlation between individual aggregation rate and initial body mass (N = 35, r = -0.17, S = 8342.7.1, $P = 0.33$) or body mass loss per day (N = 33, r = 0.11, S = 5356.6, $P = 0.56$) or with individual molt rate (N = 41, r = 0.29, S = 5039.2, $P = 0.09$).

4. Discussion and conclusion

We found an increase in surface body temperature in molting elephant seals during the mid-stage of molt in agreement with previous data on harbor seals (Paterson et al., 2012). Thus, thermal constraints of elephant seals depend on molt stage and heat loss is greatest during the mid-stage of molt. Moreover, our results showed that aggregation behavior depends on habitat type. Indeed, the proportion of aggregated seals was greatest and seals formed larger aggregations in wallows compared to beach and grass habitats. Laws (1956) and Boyd et al. (1993) already described that elephant seals prefer to aggregate in muddy wallows at South Georgia. This aggregation behavior in mud is not colony-specific, but common for this species, as long as the substrate of the site allows wallow formation. We

observed at Pointe Suzanne that wallows are created by seal aggregations within grass habitat, the weight of the animal and movement destroying the vegetation after a period of time. The grass does not grow back where wallows are formed and the same wallows are used year after year (the same wallows were observed in the quadrat since 2012). Empty wallows dry off but every season molting elephant seals move hundreds of meters from the shore to join a wallow, preferably choosing one already occupied (Chaise et al., 2018). Mud is likely to contain a mixture of soil, feces, urine and replenished by rainfall and may be influenced by heat generated from seals.

Elephant seals appear to aggregate in wallows either in search of a warmer environment or increase the temperature of the environment through local heating from metabolic heat production. Indeed, this study showed that ground temperature is higher in wallows compared to other habitats, so seals would lose less heat by conduction with the substrate in wallows compared to grass and beach habitats. Moreover, wallows are less exposed to wind than grass and beach habitats, reducing heat loss by forced convection. Our previous work found that wallows were preferably selected at initial and mid-stages of the molt (Chaise et al., 2018) when seals are shedding their old hair and skin but new hair has not yet grown. Thus, molting females experience a warmer habitat (*i.e.* wallows) when aggregating when heat loss is greatest (Paterson et al., 2012). The loss of old skin and hair and increased peripheral blood flow for cell growth are two mechanisms that increase heat loss during molt (Paterson et al., 2012). The role of fur as insulation in seals compared to blubber, is questionable but may have some value in air, mainly for pups and less for adults, but negligible in water (Kvadsheim and Aarseth, 2002; Paterson et al., 2012). The fact that elephant seals spend most of their lifetime at sea has resulted in the evolution of a diving-specialized hair structure or to provide mechanical protection of the skin surface, suggesting that fur is not an important part of their insulation (Ling 1968, 1970). However, molt stages

described in our study are based on the percentage of old hair shed (*i.e.* bare-skin exposed to air until new hair growth), and thus correspond to the visible part of the molting process (Boyd et al., 1993). The fact that aggregation behavior is less developed in grass habitat could be related to the use of grass as a transition habitat between beach and wallows, depending on molt stage and weather (Chaise et al., 2018). The variation of aggregation behavior between habitat types could be linked to the use of habitat depending on molt stage and to the sensitivity to weather conditions (*i.e.* heat loss) during the molting process (Chaise et al., 2018).

Wallows appear to be a specific and favorable habitat to molt and aggregate and aggregation behavior of molting females in this habitat was influenced by weather. Indeed, in accordance with observations of Liwanag et al. (2014) in hauled-out California sea lions, our results showed that the proportion of aggregated elephant seals (in all three habitats) and the aggregation size (in wallows) increase when weather is deteriorating. We also observed that elephant seals aggregate more during the mid-stage of molt, when cost of thermoregulation is greatest. Thus, aggregation behavior in female elephant seals appears to correspond to social thermoregulation (*i.e.* increase of huddling during unfavorable climatic conditions; Gilbert et al., 2010). Molting in wallows may also facilitate shedding of skin through physical contact/abrasion with other seals and may be an additional benefit of wallow habitats for elephant seals.

Flipper surface temperature (correlated with body surface temperature), and stomach temperature, were greater in isolated individuals compared to aggregated seals. These results suggest that huddling while molting decreases thermoregulatory costs by reducing heat loss through warming of surrounding microclimate and by decreasing body surface area exposed to air, allowing females to reduce their internal thermal set-point and corresponding metabolic heat production (Gilbert et al. 2010). However, we did not find body surface temperature

differences between peripheral and central individuals (central individuals being less exposed to heat loss). Identification of positions in the aggregation may not have been precise enough to observe an effect of reduced body surface area, or that the thermal benefits of being in the center of an aggregation are related to the aggregation's geometry (Gilbert et al., 2010). Indeed, we found that the number of central positions compared to peripheral ones (C/P ratio) increased with aggregation size, and that surface temperature of aggregated seals decreased with aggregation size in wallows, where mean aggregation size was greater than beach or grass habitats. Moreover, in grass habitat, we showed that C/P ratio of aggregations increases when weather is deteriorating, independently of an increase in aggregation size. Based on these results, it would be interesting to study in greater detail the dynamics of huddling in wallows to determine if elephant seals try to reach the center depending on their molt stage, body condition, dominance or variation in local weather (Cruwys and Davis, 1995; Gilbert et al., 2010). We observed that there were more seals in a central position than in the periphery in grass and beach habitats compared to wallows and that this difference increased with aggregation size between wallows and grass habitat. This could be related to the fact that on non-wallow habitats (*i.e.* open area of habitats), seals gather in long linear aggregations resulting in several animals located in the center. In contrast in wallows, seals follow the edges of the muddy hollow, creating a more ellipsoidal huddle.

We expected that aggregation behavior would lead to faster molt in female elephant seals. If elephant seals could renew their hair faster, they could then spend less time fasting on land and save energy (*i.e.* blubber reserves). However, we found no correlation between aggregation rate and rate of molt. A possible explanation for this may be related to the difficulty of assessing stage of molt and molt completion (Ling, 2012). Molt involves not only the shedding of skin and hair but also the regrowth of new hair (Ling, 2012). We observed only the first process and therefore may not have been able to fully assess differences in molt

completion by different individuals. Measurement of the rate of growth of new hair may therefore provide more precise estimates of molt completion in relation to aggregation behavior of females.

We did not find any correlation between individual aggregation rate and body mass loss during the molt (*i.e.* energy expenditure). The link between aggregation and energy-saving could be a more complex process (multifactorial) than the model proposes in this study. Energy-saving from thermal benefits in aggregations could be balanced with other processes such as requirements for cell growth and synthesis of new skin/hair or may be costly in terms of energy expenditure when active in huddles. The individual aggregation rate defined in this study was based on observations usually once per day which may not have been representative of individual aggregation behavior. Aggregation behavior may not be only driven by perceived cooling of the body but also by social factors. Elephant seals show high fidelity to breeding and molting sites (Laws, 1956) and we do not yet understand how aggregation behavior may be influenced by relatedness and other social aspects of conspecifics. We also measured body mass loss as an indirect measure of total energy expenditure during the molt as elephant seals were supposed fasting while on land (Crocker and Costa, 2002). However, some studies have questioned the possibility of fast-breaking during the molt (Boyd et al., 1993; Chaise et al., 2018). Other heart rate measurements, accelerometry or doubly labelled water may therefore further complement body mass loss for estimating energy use related to aggregation behavior during the molt.

In conclusion, aggregation behavior in female elephant seals was found to be influenced by environmental factors resulting mainly in differences in surface body temperature which corresponds to previously reported behavioral and physiological aspects of social thermoregulation. The thermal advantages from aggregation mainly occur in wallows that are selected as a specific social habitat where seals can benefit from huddling at the peak

of molt, when thermoregulatory costs are greatest. However, it is not clear if female southern elephant seals express huddling as an individual strategy in order to save energy during the molt. The relationship between behavioral and physiological thermoregulatory mechanisms seems more complex as body temperature and heat loss of molting elephant seals change during the molting process in association with their behavior on land. Future studies estimating the metabolic rate of animals may reveal further insights into energy savings associated with aggregation behavior during the molt, which is a relatively understudied phase of the elephant seal lifecycle.

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Conflict of Interest: The authors declare that they have no conflict of interest.

6. Ethical approval

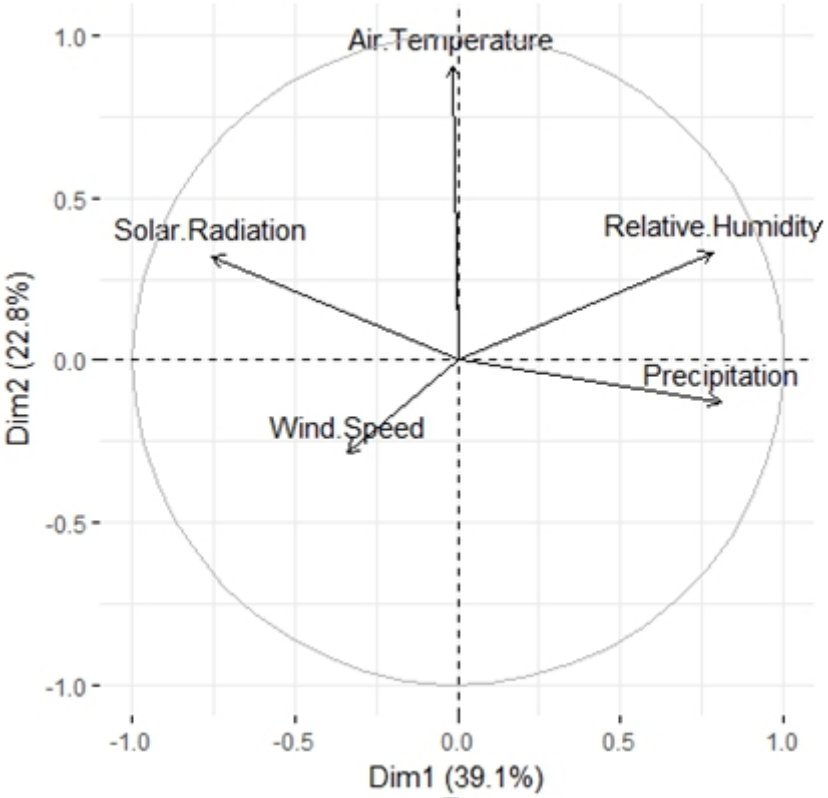
All applicable international, national and institutional guidelines for the care and use of animals were followed. All procedures performed in the study were in accordance with the ethical standards of the institution or practice at which the study was conducted.

Elephant seal work (Program IPEV 1037, HEnergES) was approved by The Antarctic Committee for Environmental Protection and the Ethic Committee (Cometh C2EA-01-FRBT: n°1037-2012, C2EA-01-FRBT: n°1037-2013; Cometh ANSES/ENVA/UPEC: n°14-055, n°15-061, n°16-078). The program was also authorized by the French Southern and Antarctic Lands (Decree 2014-131, 15th October 2014; Decree 2015-110, 4th September 2015).

7. Supplementary material

S1 Contribution to the principal components and scatter diagram of the correlation circle (visualization of the variables on the factor map; fviz_pca_var in factoextra package).

Variable	**PC1**	**PC2**	**PC3**
Air Temperature (°C)	-0.01	0.91	0.31
Relative Humidity (%)	0.78	0.33	0.12
Solar Radiation ($W.m^{-2}$)	-0.76	0.32	-0.15
Wind Speed ($m.s^{-1}$)	-0.34	-0.29	0.89
Precipitation (mm)	0.81	-0.13	0.13



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Environmental and physiological determinants of huddling behavior of molting female southern elephant seals (*Mirounga leonina*)

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Keywords: Phocids, aggregation behavior, heat loss, habitat type, meteorological variations, stomach temperature

Highlights :

- Wallows (mud pools) offer a warm and sheltered habitat.
- Heat loss of female elephant seals increases at the peak of the molt.
- A higher proportion of female elephant seals at the peak of their molt was observed amongst aggregated compared to isolated seals.
- Proportion of aggregated female elephant seals, and number of females per aggregation, are greater in wallows compared to open habitat types, and increase when weather is deteriorating.
- Gradient of surface temperature and stomach temperature are cooler in aggregated compared to isolated female elephant seals.

Figure 1

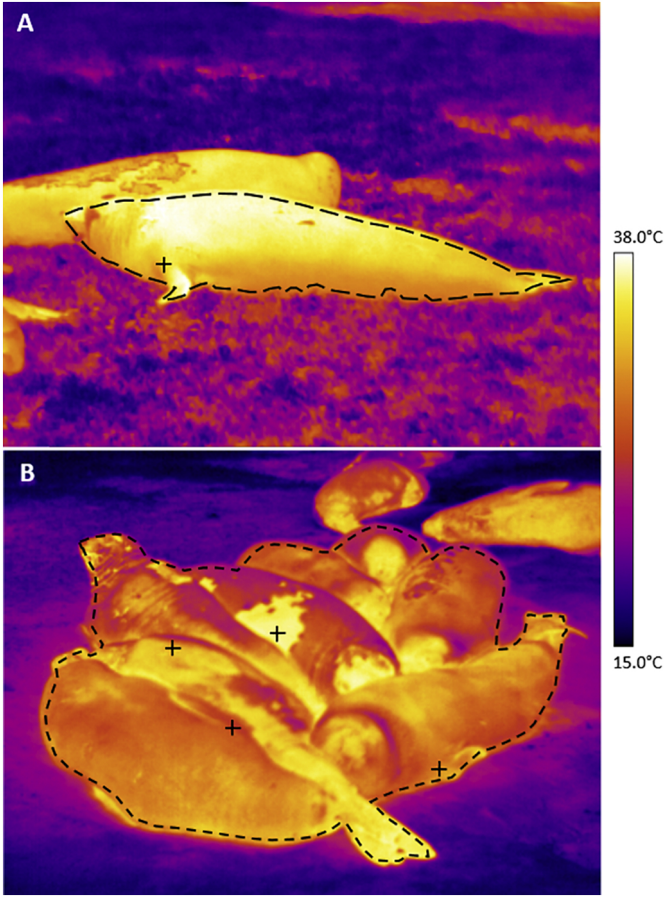


Figure 2

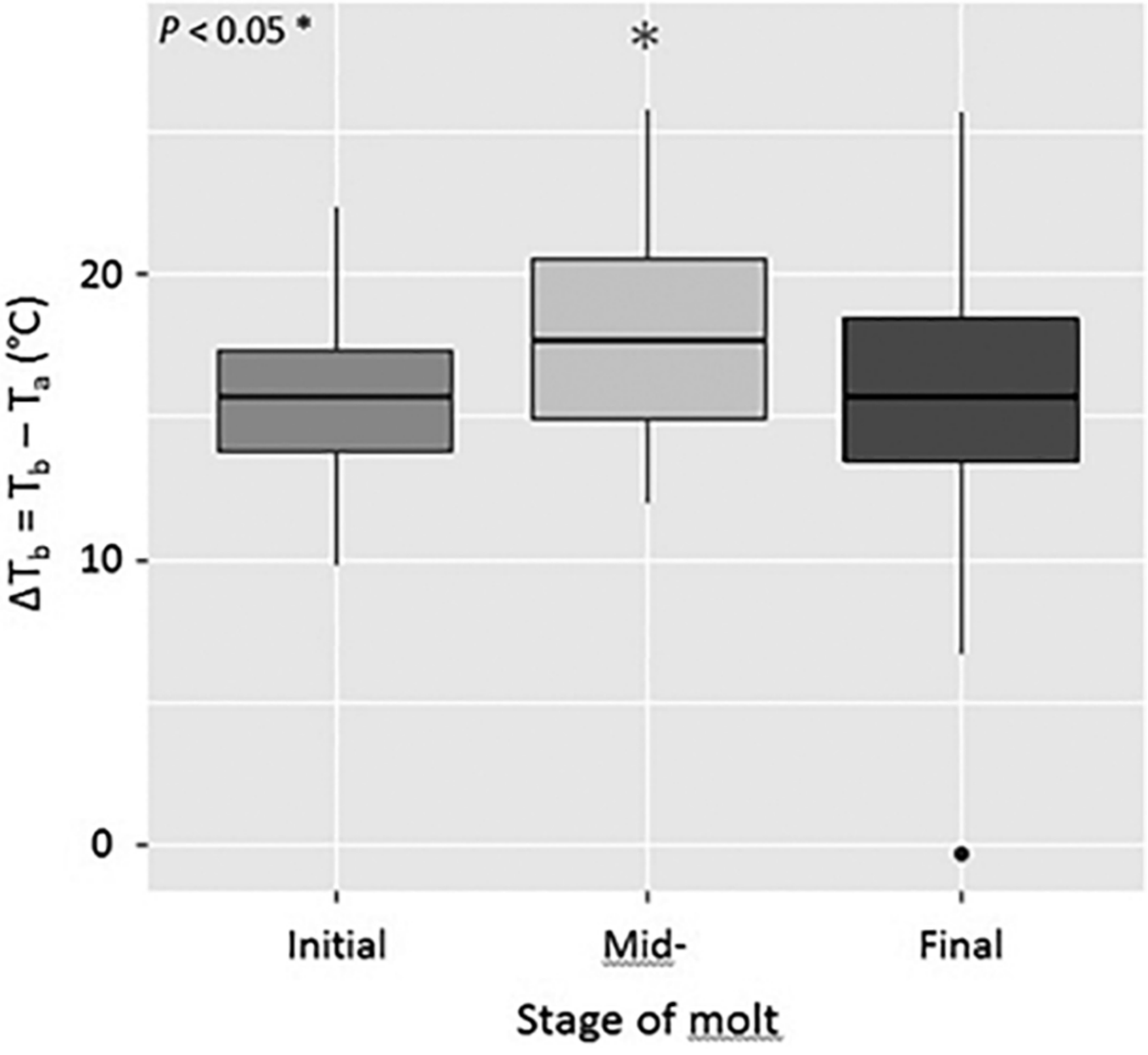
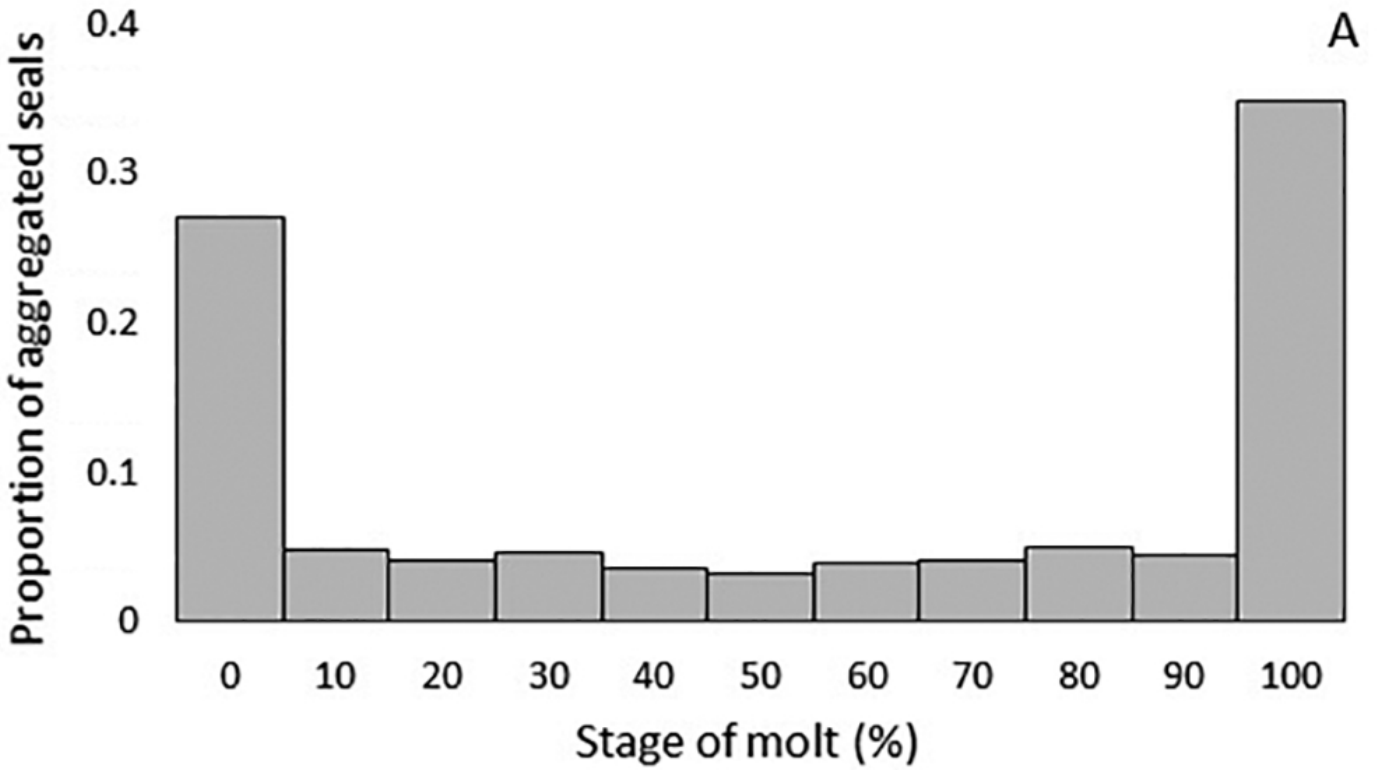


Figure 3


A
Proportion of aggregated seals
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
90
100
Stage of molt (%)

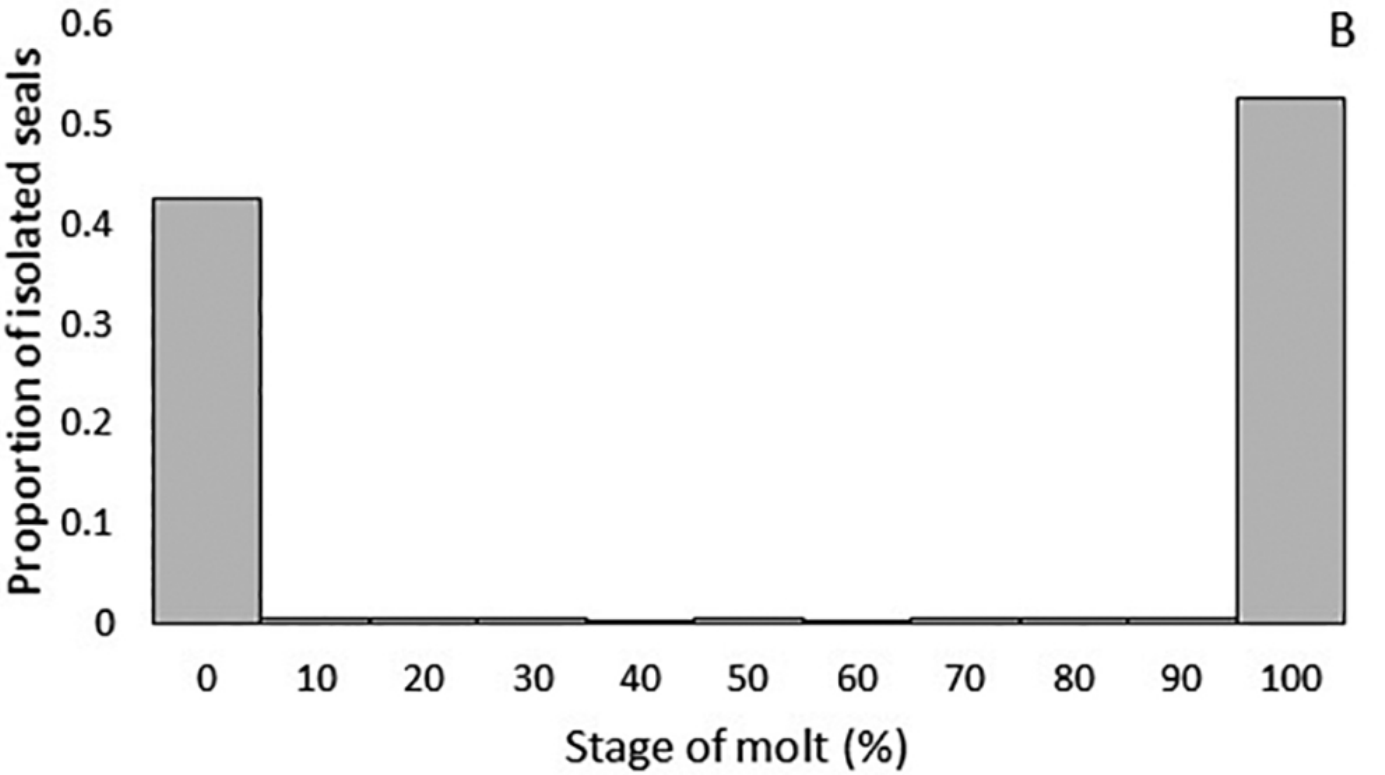

B
Proportion of isolated seals
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
70
80
90
100
Stage of molt (%)

Figure 4

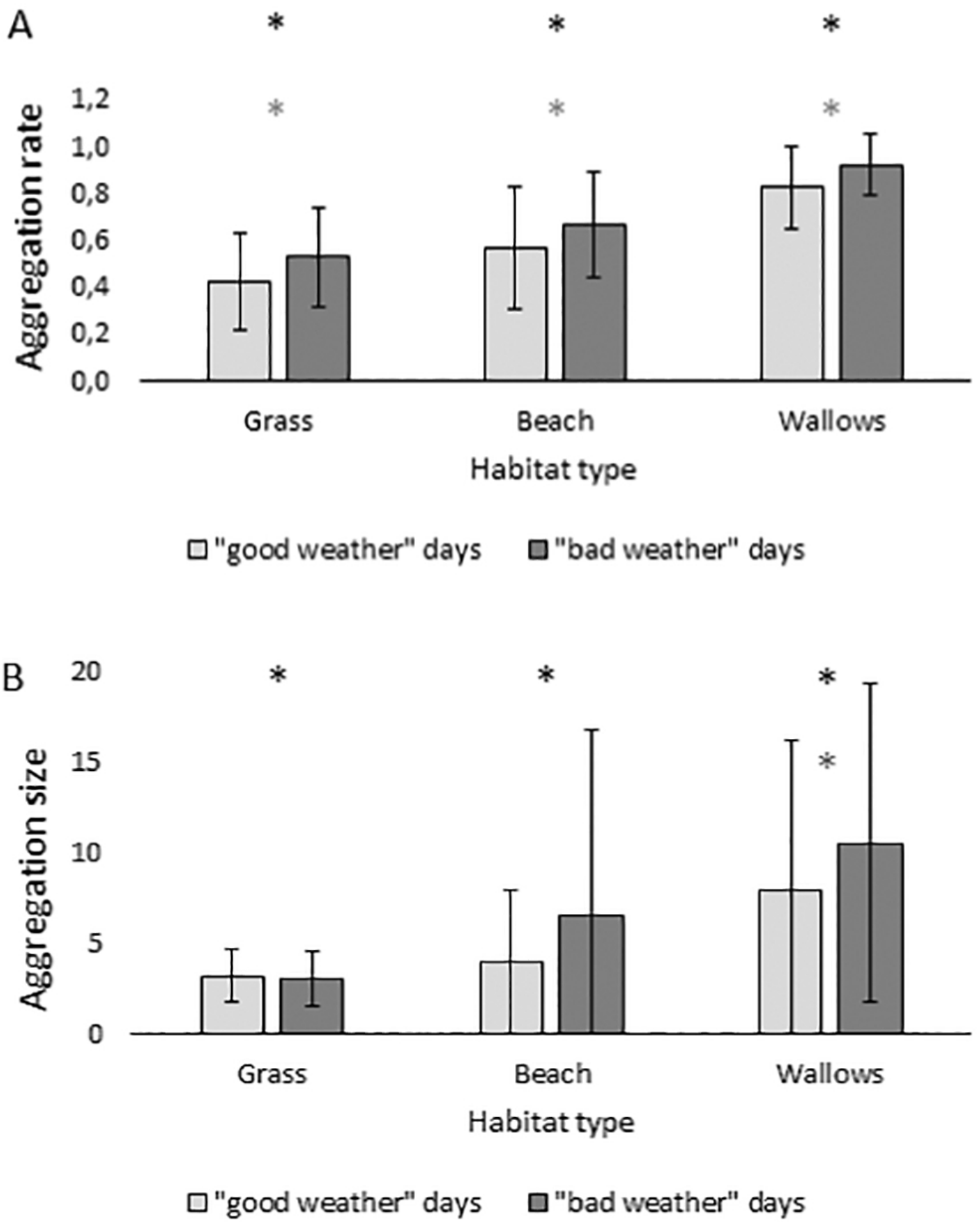

A
Aggregation rate
1,2
1,0
0,8
0,6
0,4
0,2
0,0
Grass
Beach
Wallows
Habitat type
"good weather" days
"bad weather" days
B
Aggregation size
20
15
10
5
0
Grass
Beach
Wallows
Habitat type
"good weather" days
"bad weather" days

Figure 5